THE OHIO JOURNAL OF SCIENCE

VOL. XXX NOVEMBER, 1930 No. 6

PREGLACIAL, INTERGLACIAL AND POSTGLACIAL CHANGES OF DRAINAGE IN NORTHEASTERN OHIO WITH SPECIAL REFERENCE TO THE UPPER MUSKINGUM DRAINAGE BASIN.*

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The advance of the ice brought about many changes of drainage and this seems to be especially applicable to the State of Ohio, where so many streams are running either in new channels or the direction of flow has been reversed. Many of these changes have already been explained but there is still much work to be done before a complete and satisfactory explanation of some of these problems can be presented.

My personal interest in these questions was aroused by observations made during the progress of the Reconnaissance Soil Survey of Ohio and attention was called to a few of these in a brief article in the October 23, 1914 issue of *Science*. Absence from the state for several years and the taking up of other work since my return has not permitted the following up of those suggestions as I had planned to do. Killbuck Creek, which rises north of Wooster and flows southward, offers one of the most puzzling problems of any of the streams and I have been especially interested in trying to find a satisfactory solution of the drainage in this particular section, since there is now available in the numerous borings for oil and gas positive evidence that its deep channel was not made by a stream flowing northeastward toward Orrville as suggested by Todd.† This study, however, has necessarily led me to consider, in a limited way at least, this entire section of Ohio and to some

*Paper read before the Geological section of The Ohio Academy of Science at Columbus, Ohio, April 19, 1930.

†Todd, J. H., Ohio Academy of Science, Special Papers No. 3, 1900, page 52.

extent the entire State. The subject is so large that I can only hope to offer a few suggestions, which I trust may be of help to others in the solution of these drainage problems.

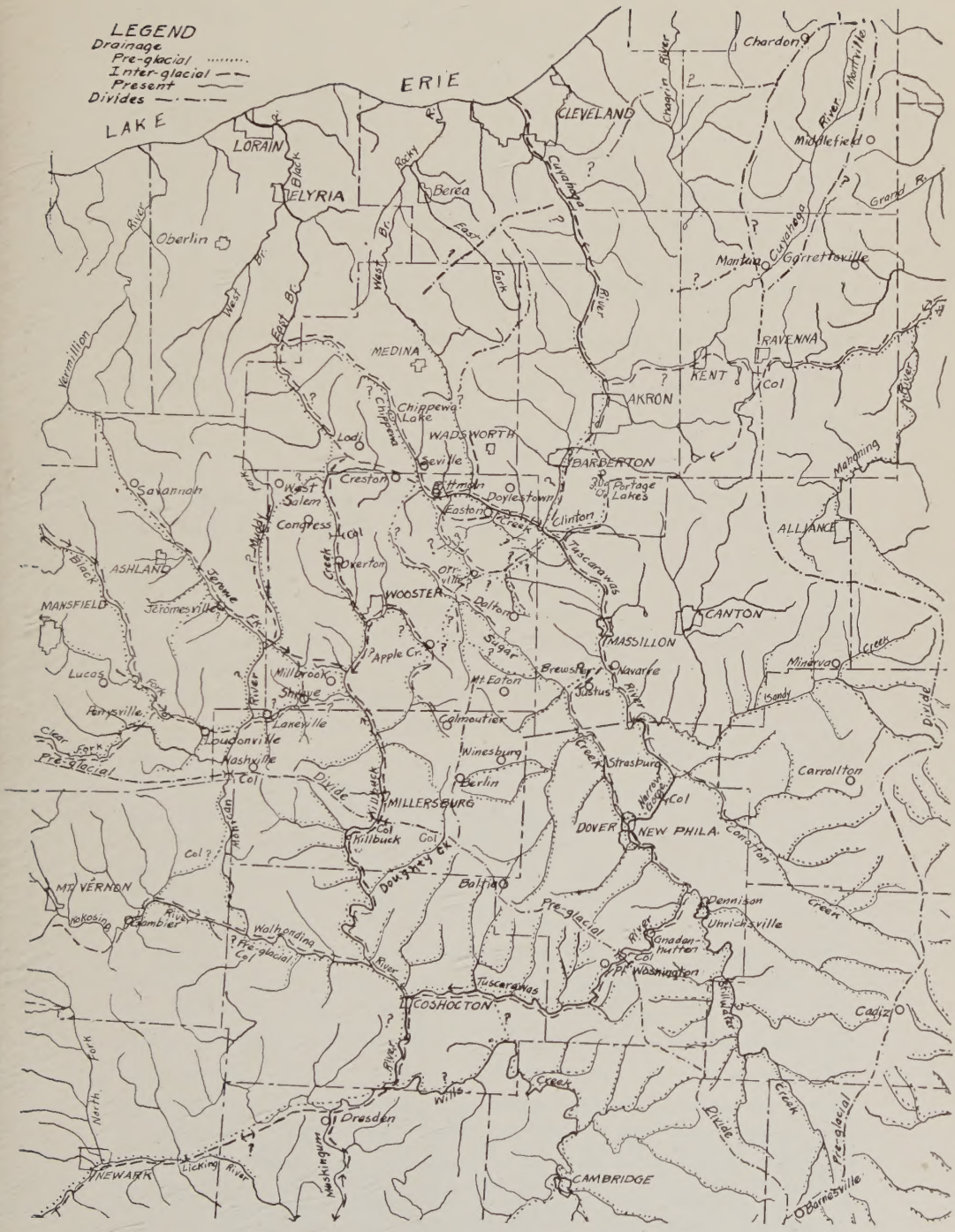
Importance of Interglacial Erosion.

In the article in *Science*, referred to above, attention was called "to the probable interglacial rather than preglacial origin of many old valleys in Ohio." Further study has tended to confirm this suggestion and, in fact, has led to the conclusion that *practically all of the deep valleys in this northeast section of the state, and probably in other sections as well, are of interglacial or postglacial rather than preglacial origin.* In other words the western extension of the plateau into Ohio had, before the beginning of the ice age, been reduced to a peneplain and the fairly stable conditions then existing were disturbed by the first advance of the ice and each successive advance caused further disturbances and changes in the drainage and resulted in rejuvenating the forces of erosion and the carving out of deeper valleys, which in many places, show little or no relation to those which existed in preglacial time.

If this suggestion represents a true interpretation of the preglacial conditions and the results brought about by the coming of the ice then it necessarily follows that it will be extremely difficult in many sections, and especially where radical changes in the drainage took place, to determine the exact location and direction of the preglacial streams. There are, however, some facts obtainable which will aid us in our investigation of this subject.

General Elevation and Slope of Uplands.

Perhaps the most important factors, which should be considered, are, (1) the general elevation and slope of the uplands, (2) the location of the main divides, valleys and streams and (3) the angle at which the tributaries enter the present stream channels, particularly in those sections where the streams were least disturbed by the ice. Topographic sheets, covering this section of the state, are now available from which it is possible to know the elevation in every part of the area. An examination of these topographic sheets shows that a very large percentage of the country lies at an elevation of from 1100 to 1300 feet. A few high points rise above 1400 feet and some of



Map of Preglacial, Interglacial and Postglacial Drainage in the Upper Muskingum Basin.

the valleys fall below 800. Nearly all of the country below 1100 feet in elevation is in the more important valleys or on the immediately adjoining slopes. The so nearly uniform height of the uplands is very strong evidence that the country was reduced to a peneplain with a surface sloping gently from the higher divides toward the broad valleys. If we can locate these old divides and valleys we will have made some definite progress in our determination of the preglacial drainage.

Location of Principal Divides.*

Geologists are pretty generally agreed that there was a preglacial divide on the present Ohio River between New Martinsville, West Virginia and Sardis in southeastern Monroe County, Ohio. From this divide the drainage was northward through the Grand River Valley to the Lake Erie basin and southward into the old Kanawha River. From the Ohio River the divide, forming the western boundary of the old Grand River drainage basin, extended northwestward to Woodsfield, thence almost directly north by Barnesville and Cadiz, passing southwest of Alliance, thence north by Ravenna, beyond which its course is somewhat uncertain as the original divide may have turned a little northeast to Middlefield, Huntsburg and Thompson or have run more nearly north near Mantua, Auburn Center and Chardon to Thompson.

The crest of this divide from near the Ohio at New Martinsville to south of Alliance is everywhere above 1200 feet and much of it is more than 1300 feet. From Alliance northward to beyond Ravenna none of it is above 1300 feet while a considerable part is between 1100 and 1200 feet. The lowest point is just south of Ravenna where it falls a little under 1100 feet, although in the valleys between Garretsville and Mantua and Parkman and Hiram Rapids the elevation is only slightly above 1120 feet. In general the elevation from Ravenna increases northward until several points again rise above 1300 feet.

*In the presentation of this paper topographic sheets, covering almost the entire area, were used and the location of the divides was brought out by coloring the areas above the 1300 foot contour line blue and those between the 1200 and 1300 foot contours red, but it is not practicable to publish these sheets in connection with this article. The accompanying map shows the present drainage and probable location of some of the preglacial and interglacial streams, divides and cols and will be of assistance in understanding the paper, although the reason for some preglacial and interglacial stream locations can only be seen by a detailed study of the topographic sheets.

From the above divide there branches off near Barnesville another one, which runs northwest to the Tuscarawas River between Port Washington and Gnadenhutten, where it is cut through by this stream; thence continues on northwestward by Baltic beyond which it divides, the main branch apparently extending westward across Doughty Creek at Troyer's Mill and is intersected between Millersburg and Killbuck by Killbuck Creek; thence continues westward south of Nashville, crossing the gorge cut by the Mohican River and following fairly closely the northern boundary of Knox County but turning a little more northwest to the plains between Mt. Gilead and Galion.

Most of the crest of this divide rises above 1200 feet and the portion south and west of Nashville often attains an elevation of 1300 feet and sometimes more than 1400 feet. A few points near Baltic and also toward Barnesville are above 1300 feet but most of the country bordering the Killbuck Valley is below 1200 feet although there are a few points less than a mile from the stream which rise above this elevation.

The other branch of this divide turns northward by Berlin to Calamoutier, where the elevation is more than 1300 feet and there are also points southwest and northeast of Winesburgh and south of Mt. Eaton which rise above this height. From Calamoutier a more or less dissected area extends northeastward almost to Dalton, beyond which its extension is uncertain for reasons which will be brought out later. The line of hills running northward from Doylestown and spreading out into a high plateau between Wadsworth, Medina and North Royalton and rising to more than 1300 feet at West Richfield and a few other points may represent its northern extension at some earlier time.

From Calamoutier the present divide turns northwestward by Weilersville, about half way between Wooster and Orrville, but the old divide may have branched off near Mt. Hope and run southwest of Fredericksburg and west of Apple Creek to Weilersville. From here it turned more to the northwest, crossed the Killbuck near Armstrong and at present swings on westward by Savannah, north of Shelby and then on southwestward and joins the highlands east of Galion. If the suggestions made in this paper are true the portion from Wayne County westward does not represent a preglacial divide but rather an escarpment, which was changed into a divide by the ice.

The evidence from the general level of the uplands seems to show that the portion of Ohio now drained by the upper branches of the Tuscarawas, Cuyahoga, Killbuck and Mohican represents an area with most of the higher portions on the south, east and north and a gentle slope from these directions toward the center and west. Differences in the hardness and dip of the rocks seems to have been the main factor in determining the general level of the uplands. *The general direction of the preglacial streams was from the southeast northwestward toward the broad plains to the west rather than from the edge of the plains southeastward into the hills as so many of them do at the present time. The former would certainly seem to be a more natural development than the latter.* If the preglacial topography was that of a peneplain, with most of the country still above an elevation of 1100 feet, such a system of drainage could have existed. This would mean that the present valleys have been very largely carved out since the coming of the ice, which hypothesis is supported by the steep slopes along nearly all the principle streams and the general youthful appearance of much of the topography and especially by the evidence of a preglacial col on the Tuscarawas near Port Washington, on the Killbuck south of Millersburg and the Mohican near its entrance into Knox County.

Probable Preglacial Drainage.

The section of the area not covered by the ice should furnish the most positive evidence of preglacial drainage as shown by the streams. There seems to be no reason to doubt that Conotton and Stillwater creeks, which rise in northwestern Belmont and eastern Harrison counties and flow northwestward to join the Tuscarawas, represent streams whose direction and location are the same as in preglacial time and that they formerly flowed on northwestward, the latter along the present channel of the Tuscarawas River and Sugar Creek, at least as far as Brewster, and the former along the present channel of the Tuscarawas, at least as far as Navarre. The old Stillwater may have turned northeastward by Justus and joined the old Conotton, flowing northward along the present Tuscarawas or the Stillwater, at least may have flowed northwestward across Wayne County to the present Chippewa Valley or more nearly westward by Kidron and Apple Creek to the Killbuck drainage. If one or both flowed northward by Massillon they may have

turned westward along the Chippewa valley or continued northward to the Cuyahoga. The southwestward course of the upper Cuyahoga and the southeastward direction of many of the tributaries of the Cuyahoga beyond Akron, as well as its failure to develop a broad valley like the Grand River, raise a question as to the Cuyahoga outlet as the earliest development of the drainage. On the other hand there seems to have been an old plain several miles in width developed along the Cuyahoga with an elevation around 1000 to 1100 feet, which seems to have been later cut into by the Cuyahoga, forming its present narrow gorge-like valley. The relatively small basin drained, as compared with the Grand River, might explain why the valley was not cut out wider and that of the present Upper Cuyahoga is probably a later glacial development.

The old divide may have extended northward from Dalton to Doylestown and the break through this west of Clinton may not have occurred until the first advance of the ice. The dip in the general level of the uplands from Medina southward and the rise again beyond Ashland seems to indicate that the drainage of a considerable area was toward the northwest along the Chippewa Valley either by Chippewa Lake or Lodi or both. The tributaries on the south side of the Chippewa Valley, as well as some other valleys in this section, practically all flow northward while those on the north side flow almost exactly in the opposite direction and it may be that the River Styx valley, Chippewa Lake and Lodi each represent separate preglacial channels which were connected together when the Grand River drainage flowed westward by Ravenna as will be explained later.

The angle at which the smaller streams enter the Tuscarawas Valley above and below Port Washington as well as an elevation of more than 1200 feet on the immediately adjoining uplands, as already pointed out, furnish very strong, if not conclusive, evidence of the existence of a preglacial divide between Port Washington and Gnadenhuten. The existence of such a divide at this point together with the narrow gorge east of Canal Dover would be absolute proof that the deepest erosion in the Tuscarawas and associated valleys took place during interglacial rather than preglacial or postglacial time and apparently at neither the first or the last advance. From this old divide the drainage was westward toward Coschocton and from there possibly westward along the Walhonding and Kokosing but

more probably along the old channel by Newark. The Kokosing and Walhonding valleys are evidently older than the Mohican, which was probably not formed until the last advance of the ice.

The Killbuck drainage is difficult to determine, as probably most of its channel has been made since the first coming of the ice. The angle of its tributaries, as well as the elevation of the uplands, seems to show the presence of an old divide south of Millersburg from which the drainage was northward at least as far as Kauke and might have flowed on by Wooster, Apple Creek and Orrville as suggested by Conrey* to the Chippewa Valley but the direction of the tributaries around and beyond Wooster as well as the unnatural turning back towards the hills seems to be against this course. The former channel through the hills to Orrville as suggested by Todd must be abandoned as data from numerous wells and ravines show this to have been impossible. The more probable channel seems to be northwestward by Millbrook and along Jerome Fork of the Mohican by Ashland and Savannah, or possibly by the Muddy Fork through the old valley, which Conrey found east of West Salem, into the valley at Lodi.

The Black Fork of the Mohican is also believed to have flowed northwest and apparently also carried the waters of Clear Creek. The drainage from Loudonville was apparently eastward to Lakeville and thence northward into the Killbuck drainage but from Loudonville westward to Perrysville was probably into Black Fork. The Mansfield drainage is also thought to have been northwestward toward Shelby. The valley, which is followed by the Pennsylvania Railroad from Mansfield to Shreve, is probably mostly of interglacial rather than preglacial origin and apparently formed the principal line of drainage for this section at the time when the valleys were being cut deepest.

The Coming of the Ice.

The advance of the ice was from the northeast along the Lake Erie basin from which it spread southward, the tendency being to flow around the higher parts of the country and spread out like fans from the larger valleys. When the ice advanced far

*Conrey, G. W., Geological Survey of Ohio, Fourth Series Bulletin No. 24, page 20.

enough southward to encounter the northern end of the divide, forming the western boundary of the Grand River basin, it blocked the northward drainage and formed a large lake extending many miles southward. This lake continued to rise until it reached the level of the lowest point in this divide, which we have already seen is just south of Ravenna. In the article referred to in *Science* it was suggested that the Pittsburg drainage first broke over at this point and that the overflow at New Martinsville was at the time of one of the later glaciations. Leverett* gives a well record at Campbellport about two miles southeast of Ravenna, which with a head of 983 feet, failed to reach rock at 230 feet, or an elevation of 753 feet above sea level. Prof. G. F. Lamb of Mt. Union College in private correspondence informs me that he has traced this old valley southwestward by Fritch Lake to the Portage Lakes. Recent well records, obtained from the Kemrow Company, show depths of 400, 404, 407 and 499 feet to rock in Sections 7 and 18 just east or south of Mud Lake, which means that the old valley floor is here around 600 feet above sea level, or little if any above the present level of Lake Erie. Another possibility was from Campbellsport somewhat northwestward along Congress Lake outlet to the Cuyahoga. From Portage Lakes an old valley extends both north and south, in fact there seems to be a network of these old valleys in the section between here and Akron, Barberton, Clinton and Canal Fulton. One of these along Nimisila Creek apparently carried the Pittsburg drainage during the earlier advances of the ice, as the narrow gorge-like valley of the Ohio seems to indicate that the present channel of this stream was not formed until later glacial time.

As the ice advanced farther west and south it blocked the drainage of other streams, which drained the plateau to the northwest, although it seems probable that the waters, which flowed across the divide near Ravenna, followed the present Chippewa valley westward by Creston and Lodi until the ice moved far enough south to force them to seek another outlet. Whether this was at the first advance of the ice has not been determined but as soon as it happened the waters from the streams coming from the southeast were dammed up and broke over the old divide on the Tuscarawas near Port Washington and flowed southwestward by Coschocton and Newark and

*Leverett, Frank Mon. XLI, U. S. G. S., page 462, 1900.

joined those from the old Kanawha, although it is possible that the first break over was along the line of the Killbuck, which might have carried the Ohio drainage until it was forced farther to the southeast.

The northwesterly flow of other streams, which drained the old plateau, were also blocked and forced to seek a way around the ice, which was found by breaking over the old divide south of Millersburg, joining the Tuscarawas at Coschocton. This Killbuck drainage seems never to have again been northward, although the Old Grand River plain was so low that the Ohio drainage probably returned to its former channel after the retreat of the ice and continued northward during one or more interglacial periods. There is also evidence for thinking that the Tuscarawas likewise drained northward by Akron into the Cuyahoga during an early interglacial period and, in fact, may have furnished an outlet for the Kanawha drainage along the old valley from Circleville northeastward by Newark to the Tuscarawas at Coschocton and then along the line of this stream and the Cuyahoga to the Lake Erie basin at Cleveland.

The Scioto valley above Portsmouth is relatively much wider than the Ohio valley below this point. The elevation of the old Kanahwa valley, whose floor is about 100 feet above the present Scioto, where it joins it at Waverly, shows that the Scioto could not have been of preglacial origin. Some obstruction may have caused the Kanahwa to break over a low divide between Portsmouth and Sciotoville so that it flowed northward along the Scioto and joined the Tuscarawas as suggested above, during the interglacial period in which the deep valleys were formed. Only by a careful study of well records will it be possible to determine the slope of the rock floor of this old Scioto-Tuscarawas-Cuyahoga Valley and it may be that it was reversed in part of its course during different interglacial periods.

Deep Valleys of Interglacial Origin.

The old Tuscarawas-Cuyahoga valley was apparently from 250 to 500 feet deeper than at the present time and this depth enabled the tributary streams like the Kokosing, the Killbuck, which then carried the Mohican, and the Chippewa to cut out deep channels also. At Cleveland the rock floor is about 500 feet below the present valley, or less than 100 feet above sea level. East of the Portage Lakes it is around 600 feet

and would probably be lower in the center of the Lakes. A well record southeast of Easton in Section 21 Chippewa Township, Wayne County, struck rock at 443 feet and another one near the same place in the northeast quarter of Section 20 entered rock at 417 feet. The elevation of the present valley here is about 950 feet so the rock floor is apparently below the present level of Lake Erie. Further west in the Southwest quarter of Section 14 Milton Township the depth was 275 feet and in the southeast corner of Section 5 of the same Township it was 262 feet. Mr. Cummings of The East Ohio Gas Company states that he drilled a well near Strassburg in Tuscarawas County 400 feet before he struck rock. Leverett reports about 250 feet or more to rock at Newark and records in Killbuck valley south of Wooster in the middle part of the northwest quarter of Section 21, Township 15, Range 13, show 206 feet although other wells only a short distance away show 82,110, 126 and 142 feet to rock. As the present Killbuck valley is around 850 feet, while Orrville is 150 feet or more above it, the valley at Orrville would have had to have been more than 350 feet deep to have received the Killbuck drainage. While wells were found east of Wooster in Section 7, Township 16, Range 12 which had depths of as much as 227 and 240 feet the surface elevation at their heads would still make the rock floor as much as 100 feet above that of the Killbuck while almost immediately east in the same sections the depth was 44, 118, 120, 160 and in Section 8 only 42 and 90. Records in Sections 3 and 4, Lawrence Township, Stark County gave 248, 260, 265 and 277 feet. A well in Section 32, Prairie Township, Holmes County, showed 298 feet but it is apparently on a gravel terrace to the west of the present valley.

It is not possible in this paper to go into any further discussion of these old valleys, which were carved out to such unusual depths, apparently during some interglacial period. The evidence given seems sufficient to show that Killbuck valley was cut out by a stream flowing southward when the Tuscarawas at Coschocton was probably 250 feet or more below its present level and not by a northeastward stream.

Drainage Changes During Late Glaciation.

The drainage, which existed when these old valleys were formed, was disturbed by another advance of the ice, probably either the Illinoisan or the Wisconsin. If the former extended

as far toward the southeast as indicated by Leverett then the change of the Ohio, Muskingum and Licking to their present channels must have resulted not later than that advance. The Wisconsin glaciation went far enough southeast to cause the drainage of the upper Mohican, which formerly flowed eastward by Big Prairie and probably Shreve to the Killbuck, to cut a gorge through the hills south of Loudenville to the Walhonding, Clear Creek being forced to abandon its course by Perryville and break through the hills to join the Mohican. By climbing the hills east of Beach City this glaciation was also probably responsible for the Tuscarawas breaking through the hills east of Dover, where it runs through a gorge across the old ridge separating the old Conotton and Stillwater valleys. The narrowness of this gorge, as compared with the width of the valleys which it connects, is one of the most striking evidences of the long period of time which passed between its formation and the breaking through the old divide near Port Washington.

Whichever advance of the ice blocked both the northern and southern flow of drainage along this old Scioto-Tuscarawas-Cuyahoga valley, forcing a new outlet through the hills along the present course of the Muskingum, with a channel much above that of the old valley, caused a damming of the streams, a filling of the valleys and the bringing about of sluggish drainage in streams like the Killbuck.

Many other interesting possibilities and details might be pointed out, if space permitted. While some of the suggestions offered may seem at first rather radical I believe that further study will show that they offer a more logical explanation of the conditions than has hitherto been presented. I trust that some of the suggestions may prove of assistance in solving the many puzzling drainage problems of northeastern Ohio.

ORIGIN OF TASTE BUDS IN THE ORO-PHARYNGEAL CAVITY OF THE CARP.

(*Cyprinus Carpio* Linnaeus).

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According to the doctrine of germ-layer specificity all nervous structures, including taste buds, are derived from the ectodermal layer of the embryo. The mucous membrane lining the digestive tract, including the pharyngeal cavity, is said to originate from the endodermal layer, whereas, that of the oral cavity is generally conceived to arise from ectoderm the presence of which is due to invagination during the formation of the stomodaeum. Most authors agree that the exact limits of ectoderm and endoderm in the oro-pharyngeal cavity cease to be distinguishable after the rupture of the oral plate. In fishes taste buds appear throughout the entire extent of the epithelial lining of this cavity. They occur on the floor, roof, and sides, including the inner surfaces of the gill arches, extending oftentimes even into the oesophagus. In spite of the difficulties in determining the exact boundaries of the two germ layers in this region, the opinion prevails that these structures are derived from ectoderm. In order to account for the presence of these so-called ectodermal derivatives in the pharyngeal cavity, a region generally conceived to be endodermal in derivation, many investigators hold to the opinion that they are derived from ectoderm which has migrated into this region either by way of the oral or the pharyngeal clefts.

Beard ('88, p. 879) claimed that he had evidence to prove that the end organs of taste arise from epiblastic thickenings which have migrated through the gill clefts into the pharyngeal cavity. Fahrenholz ('15) maintained and was supported in his contentions by Jacobshagen ('11, '12) that the oro-pharyngeal cavity in Selachians up to the commencement of the oesophagus is lined with mucous membrane derived from ectoderm. He employed the fact that placoid scales and taste buds occur in this region as evidence to support this contention.

Cook and Neal ('21, p. 48), on the other hand, claimed that in elasmobranchs "the whole pharyngeal cavity is endodermal in its origin and that there is little or no inward migration of the ectoderm into the pharynx." In regard to the origin of taste buds in this region they hold that the endoderm, within which they first make their appearance, is the active layer.

Keibel ('12, p. 183), in discussing this problem, makes the statement that "The majority of the taste buds lie undoubtedly within the entoblastic territory." For this reason he thinks that the doctrine that these structures are ectodermal in origin "is not free from objection."

Many investigators have attempted to account for the origin of taste buds in this region on the basis of their nervous innervation. Although this phase of the problem is not within the scope of the present paper some of the main contentions bearing on this point will be outlined here, since they illustrate, at least, the complexity of the problem as well as the diversity of opinion among investigators.

It has been conclusively established that taste buds in the oro-pharyngeal cavity as well as those on the external surface of the body of fishes are innervated by nerve fibers which belong to the so-called fasciculus communis system. These communis fibers have been traced from their nuclei of origin or termination in the brain, through the roots and ganglia of the cranial nerves, to their peripheral termination. It has been determined that the central termination of these communis fibers is in the vagal and facial lobes of the medulla oblongata. In the family cyprinidæ these lobes are greatly hypertrophied, the latter having fused to form the so-called tuberculum impar. The remarkable enlargement of these lobes is said to be correlated with the abundance of taste buds in the oro-pharyngeal cavity of these fishes.

We are greatly indebted to Professor C. Judson Herrick for much of our present knowledge concerning the peripheral gustatory pathways in fishes. According to this author, whose numerous papers on this subject are well known, taste buds in the oro-pharyngeal cavity are supplied by communis or gustatory fibers from the VII, IX, and X cranial nerves, while those on the outer surface of the body are supplied by the VII nerve. These results have been corroborated by other investigators for various species of fishes.

Allis ('95, '97) claimed that the fasciculus communis system in *Amia* is distributed exclusively to taste buds. Other investigators found that there are two kinds of fibers in this system each of which has a distinct distribution—one to taste or terminal buds and the other to the mucous membrane. The latter are unspecialized visceral sensory fibers ending freely in the mucosa of the digestive tract including the mouth and pharynx.

Johnston ('98, '05, '10) advanced the hypothesis that the communis system is exclusively visceral and hence endodermal, as compared with the general cutaneous and acusticolateral systems which are related to strictly ectodermal sense organs. Herrick ('98, p. 170) criticised this hypothesis on the grounds that it "seems to lead us into serious difficulties, for, in the first place, the terminal buds of the outer skin, which are very numerous in some fishes and which can hardly be other than ectodermal, are apparently all innervated from the communis system. Again, the taste buds of the mouth of fishes all or nearly all lie in the region of the stomodaeum and are therefore probably of ectodermal origin." Strong ('98 p. 173) likewise offered this criticism, at the same time suggesting that the association of gustatory fibers with visceral fibers "might be accounted for on the supposition that the end bud organs originate on or near entodermal surfaces."

Cole ('98, p. 142) at first considered the fasciculus communis fibers to belong to the visceral system, although he pointed out that it is difficult in the region of the visceral clefts to determine where the somatic region ends and the visceral region begins. In a later paper ('00, p. 320) he seems to think the opposite condition has occurred, that is, "that it was originally a cutaneous system, which has, like the early teeth, invaded the mouth."

In regard to the relationship of the terminal buds in the skin and the taste buds in the oral cavity, Herrick ('99, p. 20) pointed out that "it is generally assumed that these two classes of buds have a common origin, as well as a common structure and innervation." In a later paper ('00, p. 308) he suggested that the terminal buds are probably ectodermal in origin and that "if they arose first as gustatory organs, their migration inwards in the stomodaeum toward the tongue and teeth is intelligible. Whether the others retained this function or became tactile organs, their migration to the exposed surfaces of the body (barblets, fins, etc.) is equally intelligible."

Johnston ('05, '10) entertained an opposite view, namely that the taste organs originated in endodermal territory and secondarily spread to the outer surface of the body. He not only maintained that the evidence is all in favor of the origin of taste buds from endoderm, from the standpoint of nerve distribution, but, also claimed ('10, p. 41) that in teleosts (*Corregonus* and *Catastomus*) taste buds first appear in the pharynx and oesophagus where there seems to be no possibility of origin from any other source than endoderm."

Landacre ('07) in his studies on the time and place of appearance and the direction of spreading of taste buds in *Ameiurus melas* found (1) that they "appear simultaneously in the extreme anterior portion of the oral cavity (ectoderm) and on the endoderm of the first three gill arches," (2) that those of the pharynx spread posteriorly into the oesophagus and that those of the oral cavity spread posteriorly until they reach the pharyngeal group, (3) that no buds spread from the pharyngeal group to the outer surface of the body while the cutaneous buds, which appear later than the oral group, are continuous with the latter just inside the lips. It is evident from these results that this author confirms the occurrence of taste buds in endodermal as well as in ectodermal territory, but disagrees with Johnston's suggestion that buds spread from endodermal into ectodermal territories.

In regard to the possibility that buds in ectodermal territory may actually spread into endodermal territory, this author ('07, p. 47) suggests that this "is probably peculiar to *Ameiurus* and has no bearing whatever on the question as to where taste buds first appeared phylogenetically." However, he expressed the opinion ('07, p. 47) that "the evidence seems to be in favor of Johnston's hypothesis ('05, '06) that buds in primitive forms appear first in endodermic territory, since taste buds are always supplied by communis fibers which are visceral in their relationship as far as their central nuclei are concerned."

Another significant problem in connection with the nervous innervation of taste buds and its possible bearing on their germ layer origin is that in regard to the question as to whether the buds appear fortuitously and independent of their gustatory nerves or whether the nerve fibers take the initiative and stimulate the production of buds in the epithelium. The significance of this problem is apparent as illustrated in the case

of cutaneous and oro-pharyngeal buds which are innervated by communis fibers terminating centrally in a morphological single center and distributed peripherally by the VII nerve.

Olmstead ('20 b) and May ('25) proved by experimental methods that in *Ameiurus* degeneration of the gustatory nerve after sectioning is followed by degeneration of the taste buds and regeneration of the nerve is accompanied by the reappearance of taste buds. These authors hold, therefore, that the presence of the gustatory nerve is the causative factor in the differentiation and transformation of the epithelial cells into taste buds. Professor Landacre ('07) whose investigations on the appearance of taste buds in *Ameiurus* were embryological rather than experimental, made the significant statement in regard to the appearance of taste buds supplied by the VII nerve, that "some of these fibers on reaching the surface produce taste buds, whether in the ectoderm or endoderm."

It is obvious, therefore, that the solution of the problem as to the origin of the taste-buds in the oro-pharyngeal cavity hinges on the derivation of the mucous membrane lining this cavity. In a former paper ('29) the author published the results of a study of an embryological series of carp, ranging in age from the time the eggs were fertilized until fifteen days after hatching—the object being to determine the germ-layer origin of the oro-pharyngeal mucous membrane and its relation to the development of the pharyngeal teeth. In order to determine what germ layers contribute to the formation of the mucous membrane lining this region it was necessary to trace the development of the foregut from the earliest stages of germ-layer differentiation, and, to study the mode of formation of the mouth and gill-slits with the view to determining whether or not ectoderm migrates into the oro-pharyngeal cavity during their formation.

The results of that study presented evidence that the mucous membrane lining the oro-pharyngeal cavity consists of two types of cells each derived from a distinct source, a superficial layer of flattened cells the presence of which is accounted for by the inward migration of the epidermal stratum during development of the mouth and gill-slits, and, a deeper layer of columnar cells. The latter represents the original endodermal layer which was laid down during the formation of the primordial foregut. Furthermore, proof was offered that the enamel

organs of the pharyngeal teeth are formed from the deeper epithelial layer of the pharyngeal mucous membrane and hence are endodermal in origin. Since this was the conclusion arrived at in the case of these structures, which are considered to be ectodermal in origin, the author desired to extend his investigations to other so-called ectodermal derivatives, namely taste buds.

The taste buds in the oro-pharyngeal cavity of the carp (Fig. 1) are essentially similar in structure with those described for other teleosts. They are somewhat pyramidal in shape with the apex projecting a considerable distance beyond the level of the mucous membrane. They consist of a compact group of enormously elongated epithelial cells with greatly attenuated distal extremities and with enlarged basal ends in the region of the nuclei. As this embryological series had been stained with Delafield's haematoxylin and counter stained with eosin, no special staining technique was employed in the study of these buds. Consequently it was impossible to study the structure of the buds in great detail or to determine whether or not so-called sustentacular or basal cells were present. Neither was it possible to determine the relationship of the gustatory nerve endings with the proximal extremities of the taste cells. However, it has been conclusively established by other investigators that the sense cells of the taste bud are in contiguity and not continuous with the gustatory fibers which supply them.

The first appearance of taste buds was observed in a larva 22 hours after hatching (Fig. 2). They were immature, of course, but could easily be distinguished by means of the accumulation of cells into papilla-like structures. They bear a superficial resemblance to the neuromasts, but unlike the latter they arise as evaginations from the basal layer. Furthermore they could not be confused with neuromasts as these do not appear in this region. As can be seen in Figure 2, these immature buds are composed of columnar cells which are continuous with the lowermost epithelial layer of the mucous membrane. The cells are not as yet differentiated into sense cells but are apparently similar to the columnar cells of the basal layer of the mucous membrance with which they are continuous. The superficial flattened epithelial layer of the mucous membrane can be seen to pass uninterruptedly over these groups of proliferating columnar cells.

These primordial taste buds make their appearance simultaneously in the oral and pharyngeal cavities. This agrees with the observations made by Landacre on *Ameiurus* ('07) and is contrary to those made by Johnston ('05 and '10) on *Corregonus* and *Catostomus.* A careful examination of preceding stages failed to reveal the presence of any structures that would likely be immature taste buds.

In Figure 3 is shown a developing taste bud on the roof of the oral cavity of a larva 23 hours after hatching. This bud, with a section of a nerve shown at its base, has evaginated considerably, giving it a more or less oval shape with its cells somewhat radially arranged. By 26 hours after hatching the taste buds in the pharyngeal cavity are not only more numerous but appear to be more highly developed than those in the oral cavity. This observation is in agreement with that of Johnston ('05, '10) for *Corregonus* and *Catostomus* but disagrees with that of Landacre for *Ameiurus* ('07). Figure 4 shows one of these buds on the inner surface of a gill arch. This bud is more highly developed than in figures 2 and 3 with a somewhat oval shape. This increase in the size of the buds seems to be due to the elongation of the cells rather than by their multiplication. The cells in the center of the bud are more elongate becoming gradually shorter until at the margins they pass over continuously into the columnar cells of the mucous membrane. The distal extremities of these cells have not penetrated through the flattened epithelial covering of the bud. Neither have they assumed the attenuated shape of the typical taste cell. However the relationship of these cells to the columnar epithelium of the mucous membrane is still evident. The relation of the superficial flattened epithelial layer of the mucous membrane to the developing buds is quite apparent in these figures. It is evident that it follows their contour but apparently contributes nothing to their formation.

The next stage in the development of the taste buds is represented in Figure 5, which shows their appearance in a larva 28 hours after hatching. The entire bud is still somewhat oval in shape. However, the central cells of the bud, those which are destined to become taste cells, are considerably more elongated than those in the preceding stages. They have begun to become somewhat attenuated at their distal extremities and seem to possess an enlargement near their basal ends, due apparently to the presence of their nuclei. This central core of

elongated sense cells thus assumes a more or less pyriform-shape, whereas the entire bud with its cluster of taste cells and its covering of flattened epithelial cells possesses a somewhat oval-shape. This oval shape is apparently due to the latter layer of cells, which passes over the group of taste cells and covers it in a cap-like manner. The distal or free ends of the taste cells do not appear to penetrate the surface of the mucous membrane, but are apparently covered by the superficial flattened epithelial layer.

Figure 6 shows a taste bud at a later stage of development. This bud is found on the roof of the pharyngeal cavity of a larva 40 hours after hatching. The free extremities of the elongated taste cells have broken through the superficial flattened epithelial covering and end freely above the surface. The superficial epithelial layer, having been broken, now surrounds the attenuated ends of the taste cells thus furnishing the latter with a pore as well as a covering.

The final stage of development is shown in Figure 1, which is a mature taste bud in a larva 42 hours after hatching. The structure of this bud has already been described.

It remains then to interpret its structure in the light of its germ-layer origin. It is evident from the foregoing description of the development of the taste buds in the oro-pharyngeal cavity of the carp that the elongated taste cells are modified or differentiated columnar epithelial cells which are continuous with the lowermost layer of columnar epithelium of the mucous membrane of this region.

It has been conclusively established by other investigators that all taste buds wherever found are derived from the germinating or Malphigian layer of the epidermis. Cook and Neal ('21, p. 48) claimed that in *Squalus acanthias* "it is within the endoderm that the taste cells first make their appearance in a 45 mm. embryo by the local thickening of the epidermis and the differentiation of cells of the stratum germinativum." Keibel ('12, p. 184) in his description of the development of taste buds, claimed that "the basal cells of the epithelium lose their usual low cylindrical form and increase in size noticeably."

May ('25, p. 387) stated that when the taste buds degenerate following degeneration of the gustatory nerve "the dermal papillæ are then no longer capped by taste buds, but end among cells which do not differ in appearance from the surrounding epidermal cells." This author claimed that in the process of

formation of taste buds, following regeneration of the gustatory nerve, "it is the ordinary epithelial cells which become transformed into the gustatory cells."

A rather interesting side-light on this problem has been suggested by Botezat and Parker (quoting from Cook and Neal, '21, p. 47) namely, "that these modified epithelial cells to which the name taste buds is given may be primarily secretory, and that the nerves receive their stimulation through the response (secretion) of these cells to the stimulating substances." The latter authors go on to say that "such an explanation would rule out the term 'sense-cell' as applied to the groups of slender cells making up the taste-buds." They add further (p. 52), that if these so-called sense-cells are glandular, the deduction that all nervous receptor cells, including taste cells, are of ectodermal origin is a logical non-sequitur. However, as was suggested by May ('25, p. 404), when the Golgi method is applied to the taste buds and their gustatory nerves the former react in differential staining in the same way as the nerves themselves. It would seem therefore that these modified epithelial cells, which make up the taste buds, assume the characteristics of typical nervous receptors. In spite of this, however, the doctrine that all nervous receptors are ectodermal in origin is not in accordance with the results set forth in the present paper.

It is evident from these results that the superficial flattened epithelial layer of the mucous membrane lining this region contributes nothing to the taste bud other than a covering for the distal or free extremities of the taste cells and that, since it surrounds these extremities, it thus forms a pore. Since the author demonstrated in a previous paper ('29) that the lowermost or columnar layer of the mucous membrane, from which the taste cells are derived, represent the original endodermal layer of the foregut, therefore the conclusion arrived at here is that the taste cells, which form the taste buds, are endodermal in origin.

Summary.

1. The first appearance of taste buds in the oro-pharyngeal cavity of the carp was observed in a larva 22 hours after hatching.

2. These immature buds make their appearance simultaneously in the oral and pharyngeal cavities.

3. By 26 hours after hatching the pharyngeal buds were more numerous and highly developed than the oral buds.

4. Typical mature buds were first observed in the pharynx of a larva 42 hours after hatching.

5. These buds are essentially similar in structure with those described by other investigators for other teleosts. They are composed of elongated taste cells with attenuated extremities which project beyond the superficial flattened epithelium.

6. The superficial flattened epithelium of the oro-pharyngeal mucous membrane contributes nothing to the taste buds other than their covering and furnishes them pores whereby the attenuated extremities of the taste cells reach the surface.

7. Undifferentiated taste cells first make their appearance (22 hrs.) as low cylindrical cells similar to those of the basal epithelium with which they are continuous.

8. These cells gradually elongate and assume the shape and characteristics of typical taste cells.

9. Taste cells are therefore derived from the basal epithelium by modification or differentiation.

10. Since the author demonstrated in a former paper that the basal epithelium of the mucous membrane lining the oro-pharyngeal cavity is endodermal in origin the conclusion arrived at in the present paper is that the taste buds in this region of the carp are derived from endoderm.

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EXPLANATION OF PLATE.

These Figures are enlargements of microphotographs.
Magnification × 1800.

FIG. 1. A mature taste bud on the inner surface of a gill arch in a larva 42 hours after hatching.

FIG. 2. The first primordial taste bud to be observed in the series. Found on the roof of the pharyngeal cavity in a larva 22 hours after hatching.

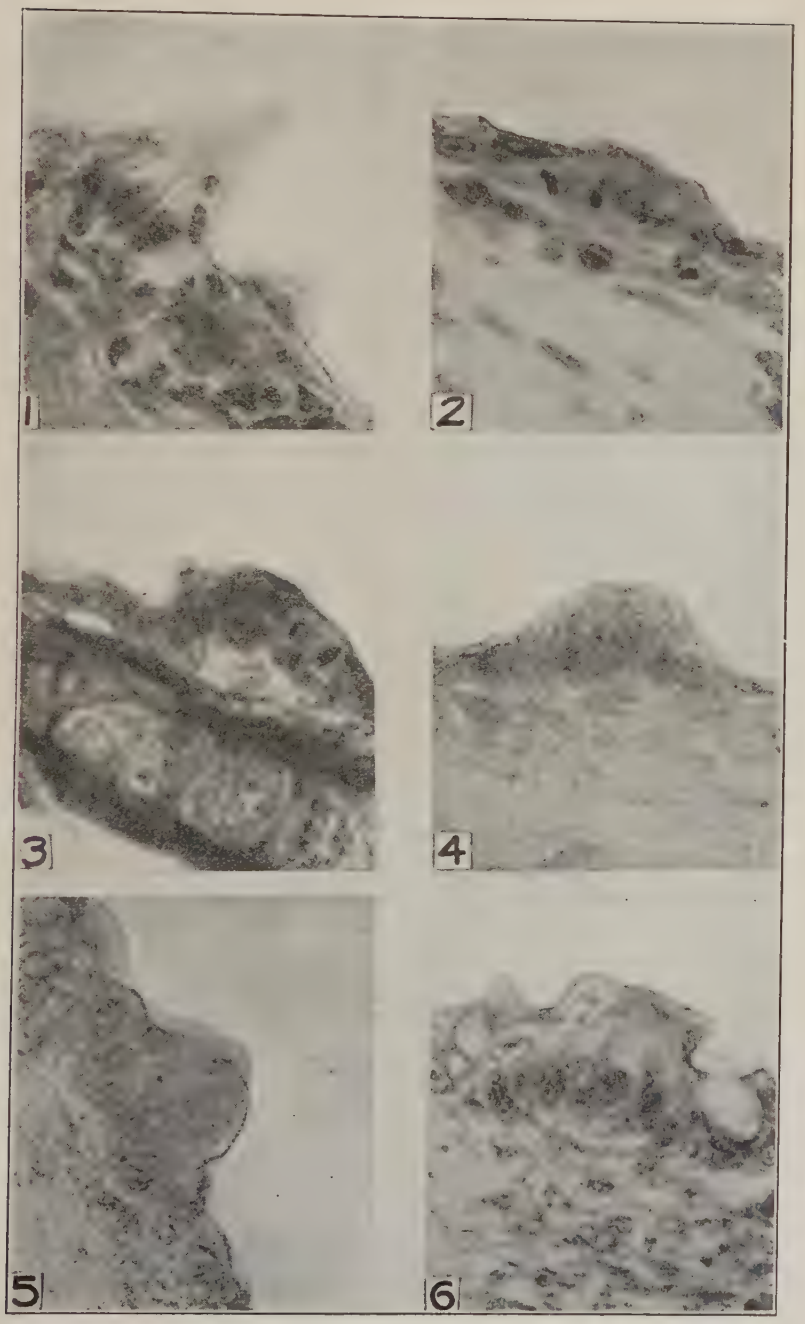
FIG. 3. A developing taste bud found on the roof of the oral cavity in a larva 23 hours after hatching.

FIG. 4. An immature taste bud on the inner surface of a gill arch in a larva 26 hours after hatching.

FIG. 5. A taste bud found on the roof of the pharyngeal cavity in a larva 28 hours after hatching.

FIG. 6. An almost mature taste bud on the roof of the pharyngeal cavity in a larva 40 hours after hatching.

NOTE.—In all these figures the superficial flattened epithelial layer of the mucous membrane lining the oro-pharyngeal cavity is comparatively easily distinguishable from the basal columnar layer. Nuclei of the cells in the former layer are shown in most of the figures, especially where this layer covers and follows the contour of the taste buds. The relation of these cells to the taste buds is quite evident in Figure 6.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VENATIONAL CHARACTERS IN TYPHLOCYBINÆ WINGS.

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The occasion for discussing this problem of wing venation of a group of small Homoptera has been brought forward by the criticism of W. L. McAtee which appeared in the Journal of the New York Entomological Society, Vol. 34, p. 158.

In commenting upon the wing drawings of Dikraneura which accompanied a discussion and revision of the genus by E. D. Ball and the writer, he makes the following statement: "The figures illustrating venation in the paper referred to are carelessly drawn in a number of instances. In general the sectors are drawn as if visible to the base of tegmen, while a leading characteristic of the subfamily Eupteryginæ is that the sectors are usually not visible basally."

Early workers referred to this basal condition of the wings as a possible character and later workers have frequently followed them without detailed work or sufficient and proper technique in study. The present criticism we trust resulted from unsuccessful attempts to examine the wings at their bases, following which it was merely assumed that this was a leading characteristic of the subfamily. Furthermore it is quite apparent by examining drawings and noting statements made, that Mr. McAtee has overlooked the veins in the basal portion of the Typhlocybid wing.

The statement that the sectors usually " are not visible basally" will not hold for the genus Dikraneura nor for the subfamily Typhlocybinæ as a whole, when thorough and careful study is made. In the genus Dikraneura the sectors are visible to the base of the tegmen in most specimens of every species examined, some more plainly than others. But even the faintest may be observed rather easily by the use of a microscope condenser. Photographs are exact reproductions of these characters, and the accompanying photographs of mounted slides of Dikraneura elytra from which drawings were made are typical examples which show the basal veins distinctly.

Many of these mounted slides were placed on demonstration at the Entomological meetings held in connection with the meetings of the A. A. A. S. at Philadelphia in December 1926.

Technique and Methods of Study.

Probably the chief reason that the veins in the basal portion of the elytra are not always seen is due to the fact that they are usually mounted on a slide in balsam for examination and when thus treated the basal one-half or two-thirds of the wing will be cleared by this solution to such a degree that the veins are not plainly visible. Especially is this true since the veins in the basal portion of the elytra are usually narrower and less conspicuous than in the apical portion. On the other hand these structures are frequently examined without removing them from the insect. In this case the veins are not visible because they are not sufficiently prominent to use reflected light and the body is too thick to use transmitted light. For these reasons if the veins are to be seen as they really exist, it is necessary to mount the elytra in a film of air and seal the coverglass without using a clearing solution of any kind. They can be kept in this condition indefinitely for further examination. These slides are then placed under the microscope which is held in a horizontal position and by the use of a 90° prism on the ocular end of the microscope, and a projection lantern transmitting the light through the objective end, the wing greatly magnified, sharply focused and with the veins showing conspicuously, is thrown on a screen and traced. In order to be as sure as possible, of these structures, the slide is then studied under the microscope and every vein is verified. The lighting factor is very important where veins are rather faintly visible since a varied degree of transmitted and reflected light will greatly change the degree of visibility. Occasionally the light when placed at an angle so as to give the effect of a dark field illumination will aid greatly in making the veins conspicuous. The drawings are then inked. All the illustrations cited as carelessly drawn were made in the manner described above after thorough study and care, with the exception of three which were made from unique types where the wings could not be removed. One of these is in the private collection of W. L. McAtee at Washington. The writer is not certain of the correctness of these three illustrations. In all other

cases the drawings were made as cited above and although errors may have occurred, care was exercised in an attempt to portray the venation correctly.

Discussion.

In further commenting upon the drawings of Dikraneura wings he states "no fewer than six different styles of fusion of

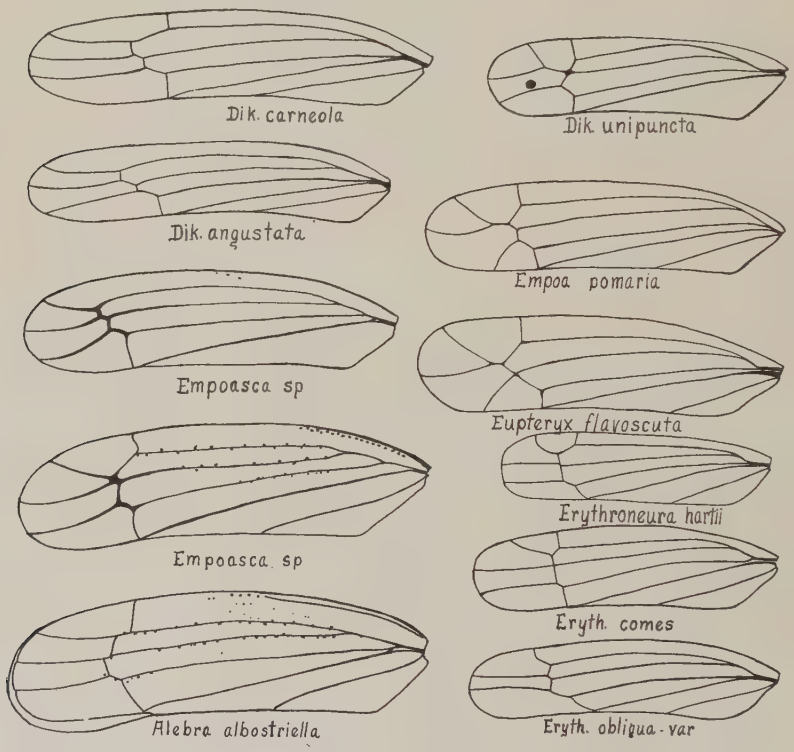

Fig. 1. Venation in Typhlocybinæ.

these veins basally are shown; a state of affairs which if actually exhibited by the specimens would compel their distribution to widely separated taxonomic groups." These groups are not named and we are left in doubt as to their identity.

This criticism is especially interesting since on the same page of his paper and in referring to a variable character in the apical portion of the wing, used for a generic separation, he states that it is "too variable to serve as the basis for such a

trenchant character." When these variations are pointed out by another worker however no consideration is given to them, the variation would be absurd and the specimens would be placed in widely separated taxonomic groups.

The point in question here is very similar to that at the apex of the wing, a question of the distance of the point of fusion of veins from the base of the wing, and which veins unite farthest from the base. This is apparently quite variable or seems to be as one studies it in a series of specimens. When species and genera are considered the variation is even greater.

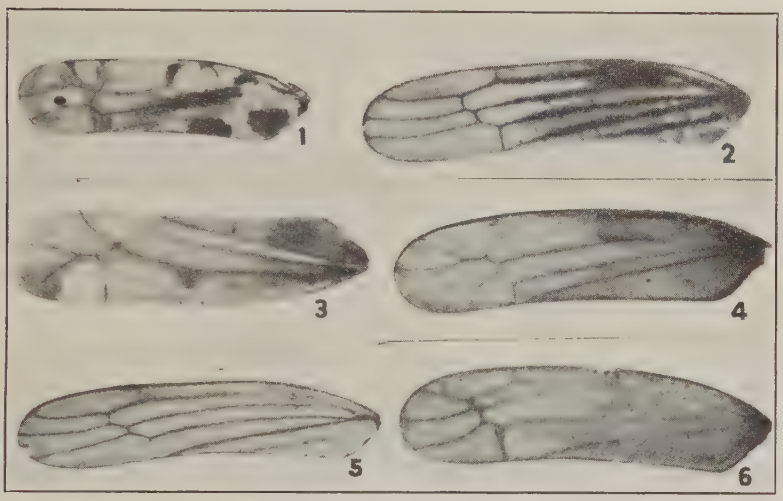

FIG. 2. Venation as shown by photographs.

Regardless of what the original condition may have been, we must study the present fusion of veins as we find it and must not assume that certain types of fusion would widely separate certain species unless we can prove it.

The great majority of Typhlocybid wings display the type of venation at the base as seen in *D. carneola* and *D. angustata* where "R" and "M" unite at the base before their fusion with "Cu" or the apparently united veins "Cu" and "1st A". This apparently is the rule, but there are exceptions. In some cases "Cu" will bend very sharply toward "1st A" and either unite with it or run parallel and proximal to it. Occasionally it bends sharply back and unites with "R" and "M" which are fused beyond this point. In some cases "R," "M," "Cu"

and "1st A" all seem to unite or fuse at about the same distance from the base, or if not fused, run parallel and so close to each other that the microscope does not designate them as separate veins. Perhaps the most interesting or peculiar condition is a fusion spur that occasionally unites "1st A" and the main trunk of "R" and "M" just beyond or at the point of fusion with "Cu." This is confusing in many instances if one attempts to trace the fusion point of "Cu."

In the case of *D. unipuncta* "R" does not fuse with "Sc" but runs very close to it and fuses in the usual manner with "M." In the drawing previously published by the writer the fusion portion at the base was omitted and the drawing was misleading. The second anal vein is frequently absent in the wing.

In certain species of *Alebra*, *Empoasca*, *Empoa* and *Erythroneura* "R" and "M" are frequently shown only faintly on the disc of the elytron and these faint veins are closely bordered by a row of pits or tubercles. The fusion of these veins basally is usually plainly visible or conspicuous. By properly focusing and adjusting mounted wings these veins can be traced in pratically every case from the apical portion of the wing where they are most prominent to their points of fusion at the base.

In view of these facts it would seem that the criticism was unjust and furthermore it would seem absurd to state that a drawing was "carelessly made" if one had never seen the structure which another was attempting to illustrate and knew nothing of the care exercised and the methods and technique employed in an attempt to describe and portray the structures present.

TEMPERATURE GRADIENT IN THE EGG-LAYING ACTIVITIES OF THE QUEEN BEE.

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Introduction.

It is generally thought that the hive temperature at which the queen is stimulated to start her egg-laying activities in early spring is about 93 degrees F. One might gather from this that when brood-rearing has once been stimulated the above temperature is maintained in the brood nest, and that the queen is rather fixed in responding by egg-laying at any other than the temperature stated. It was because of some doubt concerning this idea that this study of the gradient in egg-laying was undertaken.

The writer wishes to express his appreciation to Professor Herbert Osborn for his helpful suggestions on this work.

Apparatus.

The thermocouple method of taking temperatures lends itself admirably to this type of work. The use of these instruments avoids any abnormal reactions which might result in stimulating the colony and thus causing a higher temperature which was often the case in the old method of taking temperatures with mercuric thermometers. Also the readings are accurate and almost instantaneous.

A two pound package of bees with an untested queen was placed in a four frame vertical observation nucleus. Before any study was undertaken, the bees were left long enough so that they had become fully adjusted to their environment and had begun broodrearing. The four frame vertical observation nucleus consisted of four Hoffman frames placed one above the other. The sides of the observation nucleus were of glass. On Each side of each frame were three thermocouple junctions inserted through the glass, making six junctions for each frame and twenty-four for the entire nucleus. (See Fig. 1, for arrangements of the thermocouple junctions). This observation nucleus was placed in a dark room where the temperature was

quite constant. Red lights, to which bees made no abnormal response, afforded illumination for the worker to carry on his observations. An extension of the entrance of the observation nucleus was made which led to the outside of the building and thus allowed flight activities for the bees.

FIG. 1. GENERAL ARRANGEMENT OF APPARATUS WHEN STUDYING THE EGG LAYING ACTIVITIES OF THE QUEEN BEE.

GENERAL PROCEDURE.

Observations on this experment which were carried on in 1928 were begun on the morning of June 5th and continued through the evening of June 9th. These observations were arranged in three thirty-minute periods daily; one in the morning, one at noon, and one in the evening, so as to obtain a fairly accurate representation of what took place during each day.

In the study of the gradient in the egg-laying activity of the queen bee, observations were taken on the amount and position of the brood and the bees; the number of eggs laid by the queen; the exact position of these eggs, and the temperature of the region in which the eggs were laid. After these data had been gathered for the entire period, they were arranged in a temperature gradient table which started at 73 degrees F. and with intervals of 3 degrees (ie. 73-76-79 etc.) culminated at 94 degrees F. At these various temperatures, the number of eggs laid during the observation periods were tabulated (Table I). Fig. 2 gives a graphic representation of the tabulated data.

TABLE I.

INFLUENCE OF BROOD NEST TEMPERATURES ON THE EGG LAYING ACTIVITY OF THE QUEEN BEE.

TEMPERATURES DEGREES F.	71½° 73°	74½° 76°	etc. 79°	82°	85°	88°	91°	94°
Number of eggs laid by the queen.....	0	2	19	34	67	110	96	22

DISCUSSION.

As shown in the table, the egg-laying activity of the queen was carried on from 73 degrees F. to 94 degrees F. thus showing conclusively that after the queen has once started her egg-laying activities in the spring she is not absolutely confined in her egg-laying processes to a rather narrow range of temperatures. However, the temperature range is relatively very narrow at which she responds most actively to egg-laying, as shown in Table I. This region ranges from 88 degrees F. to 91 degrees F. It is interesting to note the gradual gradient from the optimum egg-laying temperature to the lowest egg-laying temperature. Of equal significance is the egg-laying gradient from the optimum temperature to the highest temperature recorded or 94 degrees F. A comparison of the gradient in egg-laying taking place from the optimum to the lowest temperature with that from the optimum to the highest temperature indicates that the fall of the gradient in egg-laying is

much greater in the latter than in the former. This is further substantiated in some observations already reported.*

During the observation period, other factors were recorded which must be given careful attention in order to make a clear diagnosis of the gradient in the egg-laying of the queen bee.

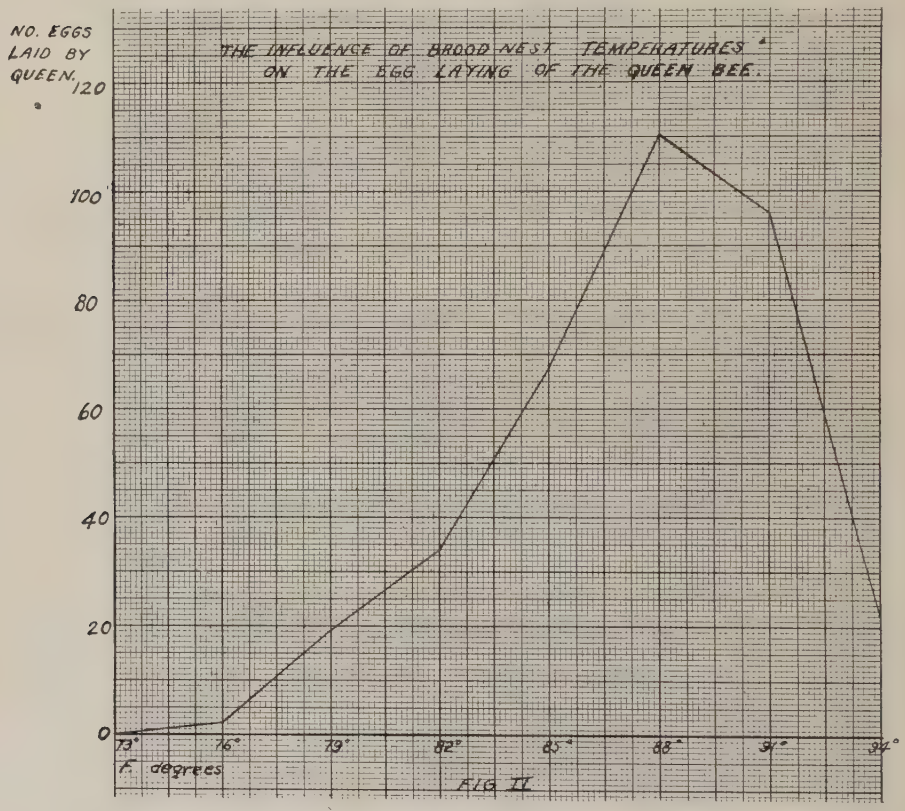

FIGURE 2.

The fact must not be overlooked that this experiment was conducted during the spring when brood-rearing is more intensive than at any other time of the year. When conditions are normal, as was the case in the colony used in this experiment, there is a rapid expansion of the brood-nest. Because of the ability of the queen for heavy egg-laying during

*Dunham, W. E. The Relation of Heat to Brood Rearing. Gleanings in Bee Culture. 57: 359–362. June, 1929.

the spring period, she not only keeps the area from which brood is emerging filled with eggs, but she also lays eggs on the outer region of the brood-nest, thus constantly increasing the area occupied with brood. It is quite evident that the warmest temperatures will occur in the central region of the brood-nest and that the cooler temperatures at which the queen will lay, will occur at the junction of that portion of the comb unoccupied with brood with that containing brood.* Thus it is obvious that when intensive brood-rearing is going on which results in a rapid expansion of the brood-nest, the gradient in egg-laying from the optimum temperature to the low extreme will cover a wide range.

Having made a detailed study of the egg-laying gradient for this particular period of the year, certain correlations are suggested. Nolan's work brings† out very conclusively that there are definite phases in the brood-rearing curve during different parts of a year. In brief, he found that there are three distinct phases of the curve, which are: the initial brood-rearing phase, the major brood-rearing phase, and the contraction brood-rearing phase. Following the latter is a broodless period.

The initial brood-rearing phase begins early in the spring and follows the broodless period which might be termed a semi-dormant phase. In comparing the amount of brood present at this time with the number of bees to care for it and maintain the other activities of the hive, it is obvious that the ratio of the number of bees to the amount of brood is very high. As a result, the temperature where the queen begins laying would be quite constant. This would mean, then, that the temperature gradient in egg-laying would be confined to a small area with a slight temperature range. However, as the brood-nest becomes more and more expanded during this initial brood-rearing period, the range in the temperature gradient in egg-laying would become increasingly greater. The reason for this is that, as the brood-nest is rapidly expanding, the ratio of the number of individual bees to care for the increasing brood area and carry on the other activities of the hive becomes less and less. When this ratio has reached its

*Dunham, W. E. The Influence of External Temperature on Hive Temperatures during the Summer. Journ. Econ. Ent., 22: 798–800. 1929.

†Nolan, J. W. The Brood Rearing Cycle of the Honey Bee. U. S. Dept. Agric. Bul. No. 1349.

extreme, the temperature gradient in egg-laying from the optimum temperature to the low temperature will reach its widest range. As the brood emerges, and the ratio of the number of individual bees to care for the brood and the duties of the hive increases, the range in the temperature gradient of egg-laying becomes increasingly less. Also correlated with the increasing number of bees in a hive is an increase of the temperature in the central upper portion of the brood area to more than the optimum temperature regardless of the activities of the bees which tend to hold the temperature rather constant. The fact must not be overlooked that some heat is given off by the brood due to its metabolic activity.

Another interesting correlation occurring during the initial brood-rearing period is the difference between weak and strong colonies in the temperature gradient in egg-laying. In weak colonies this gradient from the optimum temperature to the lowest temperature covers a wider range of degrees and is also extended over a longer period of time than is the case in strong colonies. Because of the small number of bees in weak colonies, the queen soon has the area of the hive filled with brood where the bees are able to maintain a favorable temperature. In such a case, because of the tendency for a rapid expansion of the brood-nest, the queen responds by laying in cooler temperatures than she would otherwise.

The recommendation of beekeeping experts to leave packing on colonies until weather conditions in the spring have become settled, also has a direct influence on the temperature gradient in the egg-laying of the queen bee. With this insulating layer around the hive, the bees are able to maintain the favorable egg-laying temperature over a larger area of the hive, than they could otherwise. This would result then in the temperature gradient in the egg-laying of the queen covering a narrower range from the optimum temperature to the lowest temperature than if the colonies were unprotected and consequently she would lay eggs at a much more rapid rate.

Another interesting phenomenon which takes place during the initial brood-rearing period is that, as one goes northward from the southern states, the intensity of brood-rearing becomes increasingly greater. It has been suggested that the intensity of brood-rearing increases as the length of the broodless period increases. The writer is not in accord with this belief but

attributes it to certain other conditions found in the northward regions.

The writer is of the opinion that if a queen were taken from a northern colony where the broodless period had been long and placed at the beginning of the initial brood-rearing period in a colony in the south, that the intensity of brood-rearing and magnitude of the initial brood-rearing curve would undoubtedly correspond very closely to that of other colonies in the south where the queens had been wintered over with the colony and the broodless period had been short. It has already been shown that if a queen from the south where the broodless period had been short were introduced at the beginning of the initial brood-rearing period to a colony in the north, the intensity in brood-rearing and the magnitude of the initial brood-rearing curve would correspond very closely to that of other colonies in the north where the queen had been wintered over with the colony. A good example of this is the practice among northern beekeepers of sometimes buying from the south, pound packages of bees with a tested queen. The bees are young and have never passed through a broodless period which eliminates any possible argument that over wintered bees factor in the magnitude of the initial brood-rearing curve in the north. However, the queen in order to be of a tested grade and shipped out this early in the season must have been reared the previous year and have passed through a southern winter where the broodless period is short. A package of bees with a tested queen which is shipped so that it begins brood-rearing about the same time as brood-rearing starts in northern colonies, begins brooding just as intensively and the final peak in the initial brood-rearing curve reaches the same magnitude as in northern colonies where the broodless period has been long. It is quite evident then that the length of the broodless period is not the determining factor in the magnitude of the initial brood-rearing curve but that there are other conditions that are present as one goes northward that are not present in the southern states which have a direct bearing on the magnitude of the initial brood-rearing phase. One of the important factors which has a direct bearing to some degree at least on the temperatures that occur within the hive must be external temperatures.

As one goes northward, the temperatures occurring in early spring when brood-rearing starts, increases gradually as the

season advances. Thus it requires a longer time before external temperatures occur which are as high or higher than the optimum egg-laying temperature. Because of these cooler conditions, even though the population of the colony increases, there is a longer time for the queen to lay on the lower scale of the optimum egg-laying temperature as well as at the optimum egg-laying temperature. Since the gradient is much slower on this side of the scale, it results in the fact that the initial brood-rearing curve will reach a high magnitude.

In the south one finds a reverse condition. The temperatures occurring in spring when brood-rearing starts, increase quite rapidly as time goes on and so in a short time external temperatures occur which are as high or higher than the optimum egg-laying temperature. Because of these higher temperatures along with the increased population of the hive, there is a large portion of the hive where the temperature is on the higher scale of the optimum egg-laying temperature. Since the gradient is much more rapid on this side of the scale, the initial brood rearing curve will not reach a high magnitude.

NOTES ON THE ODONATA OCCURRING IN THE VICINITY OF SILVER LAKE, LOGAN COUNTY, OHIO, FROM JUNE 25 TO SEPTEMBER 1, 1930.

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Most of the collecting during the summer was done on or around Silver Lake (also called Lake Mac-O-Chee), a lake of about 75 acres located three miles west of Bellefontaine, at an elevation of 1090 feet. The highest point in the state, 1550 feet, is located about five miles northeast of this lake. Collections were made at other points as follows: Black Lake, a smaller lake two miles southeast of Degraff (one trip, July 15); along Buckongahelas and Bluejacket Creeks northeast of Degraff (several trips); in numerous swampy woods and ponds within a radius of four or five miles of Silver Lake (several trips); along the North Fork of the Miami near Indian Lake and in the marshes at the northeast of Indian Lake (one trip, July 24); along Mad River just south of Zanesfield (one trip, July 18); at Cedar Swamp, about five miles south of Urbana in Champaign County (two trips, July 22 and August 13); and along Mad River just south of Urbana (one trip, August 13). In spite of the fact that several trips were taken along the creeks west of Silver Lake and along Mad River, no gomphines were observed or taken. Apparently the trips were made too late in the season for these species.

There follows an annotated list of the species taken or observed:

Family AESCHNIDÆ.

Subfamily Aeschninæ.

1. **Anax junius** Drury. Fairly common near ponds and lakes throughout the summer. Last observed in tandem July 4.
2. **Aeschna umbrosa** Walker. Common throughout the summer on small ponds and in woody swamps. A few specimens were taken around the lake (Silver Lake).

Family LIBELLULIDÆ.

Subfamily CORDULINÆ.

3. **Epicordulia princeps** Hagen. Fairly common up to about the middle of July. It flies over the open water of the lake near the shore.

Subfamily LIBELLULINÆ.

4. **Nannothemis bella** Uhler. All the specimens of this species were taken at Cedar Swamp, where it was quite abundant. These little libellulines occur in the marsh grass in the open part of the swamp, rarely if ever flying above the top of the grass. They hover in the midst of the grass a foot or two above the ground, and then very suddenly—sometimes so quickly that the eye can scarcely follow the movement—they dart away and hover over another spot a few feet distant.
5. **Perithemis tenera** Say. Abundant throughout the summer. This species was most abundant around patches of yellow pond lilies, and one female was observed ovipositing in the water contained in a little pool formed by a lily leaf. Another was observed ovipositing on a piece of submerged vegetation. Though most abundant over water and around the lily pads, where they apparently never fly more than a foot or two above the water, they were occasionally taken in the marsh grass near the edge of the lake.
6. **Celithemis eponina** Drury. Only one specimen of this species was seen during the summer; it was observed flying over an open field about a mile northeast of Indian Lake, July 24.
7. **Celithemis elisa** Hagen. This species was observed occasionally during the summer, flying over the open water two or three feet above the surface, and sometimes alighting on cattails or bushes at the water's edge. A few were observed in tandem, but none ovipositing.
8. **Libellula luctuosa** Burmeister. Quite common on lakes and ponds throughout the summer.
9. **Libellula pulchella** Drury. Quite common throughout the summer near lakes, ponds, and streams, and occasionally observed three or four miles from water.
10. **Plathemis lydia** Drury. Quite common throughout the summer, occurring in situations similar to those in which the preceding species was found.
11. **Sympetrum obtrusum** Hagen. Three males were taken during the summer, June 28, July 1, and July 24, in swamp grass and swampy woods near the lake.
12. **Sympetrum rubicundulum** Say. Abundant throughout the summer. Occurs almost everywhere except over the open water of the lake.

13. **Sympetrum semicinctum** Say. Fairly common throughout the summer in fields near the lake.
14. **Sympetrum vicinum** Hagen. The first specimens were taken July 28. From that time on they were quite common, occurring most abundantly at the outer edge of the swamp and in fields near the lake.
15. **Leucorrhinia intacta** Hagen. This species was fairly common up until July 4, when the last specimen was taken. Most of the specimens were taken in cattails at the edge of the lake.
16. **Pachydiplax longipennis** Burmeister. This species was quite abundant up until August 1. It was most abundant in the cattails at the edge of the lake, but specimens were occasionally taken in the woods and fields some distance from the lake.
17. **Mesothemis simplicicollis** Say. This species was quite abundant up until about August 1. Most of the specimens were taken in fields near the lake and at the outer edge of the weeds around the lake, but this species is also quite common in the cattails at the water's edge.
18. **Tramea lacerata** Hagen. This species was observed occasionally up until July 4. It flies several feet above the surface of the water or land.

Family AGRIONIDÆ.

19. **Agrion maculatum** Beauvais. Abundant throughout the summer along small streams or ditches which are edged by or filled with thick vegetation.
20. **Hetaerina americana** Fabricius. Quite common from July 8 on, along small streams containing ripples. It flies close to the water and alights on the vegetation overhanging the water. The flight is very quick and rather irregular. Two males will frequently fly across the ripples, flying in circles around each other.

Family COENAGRIONIDÆ.

Subfamily LESTINÆ.

21. **Lestes eurinus** Say. One male, July 3, taken in a swampy woods.
22. **Lestes congener** Hagen. Several specimens, July 3 and 8, chiefly in swampy woods. One specimen was taken at the edge of a fairly dry (oak-hickory) woods some distance from water.
23. **Lestes unguiculatus** Hagen. Fairly common from the middle of July on. The specimens were taken in grassy swamps.
24. **Lestes forcipatus** Rambur. Specimens were taken occasionally during the summer in marsh grass or in woods near the marsh.
25. **Lestes rectangularis** Say. Quite common up until August 1 in the marshes and woods around the lake. This was the most abundant species of Lestes observed during the summer.

26. **Lestes uncatus** Kirby. Several specimens taken from July 1 to 8 in swampy woods.

Subfamily COENAGRIONINÆ.

27. **Argia apicalis** Say. Numerous specimens of this species were taken at Indian Lake July 24. Some were taken in tandem flying at the water's edge close to the surface, or alighting on the vegetation bordering the water. Others were taken alighting on bare ground, fallen logs, and the like not far from the water. In the open, away from the water, their flight seems to be quicker, and they are rather difficult to capture.
28. **Argia bipunctulata** Hagen. This species was taken at Cedar Swamp. It was quite abundant in the marsh grass in the open part of the swamp on the first trip, July 22, and much less abundant August 13. The flight is rather weak; they are not at all difficult to capture. Their flying is confined to the marsh grass; they never seem to fly above it.
29. **Argia tibialis** Rambur. One pair in tandem taken July 24 at Indian Lake.
30. **Argia violacea** Hagen. Specimens were taken from July 8 to August 5. It was fairly common along Buckongahelas and Bluejacket Creeks, where it seemed to prefer the vegetation along the edge of the stream. One male was taken in the marsh grass at Black Lake, July 15.
31. **Amphiagrion saucium** Burmeister. Numerous specimens of this species were taken at Cedar Swamp, where it was quite common, especially in the grassy part of the swamp.
32. **Nehalennia irene** Hagen. Fairly common up until August 1 in the grassy part of the swamps surrounding the lake. One female was taken at the edge of a fairly dry (oak-hickory) woods about half a mile from the lake.
33. **Enallagma hageni** Walsh. Two males, June 26 and 28, taken in the cattails at the edge of the lake.
34. **Enallagma geminatum** Kellicott. Two males, July 24, at Indian Lake, and numerous specimens in the bulrushes at the water's edge at Silver Lake the last week in August.
35. **Enallagma signatum** Hagen. Quite common throughout the summer, occurring over the open water of the lake, and occasionally back in the marshes. It is most abundant flying a rod or so from the edge of the cattails or marsh grass, a few inches above the surface of the water. Oviposition, on submerged vegetation, occurs in tandem. The female alights on the vegetation and the male holds itself up at an angle of about 45 degrees while the female lays her eggs.
36. **Enallagma vesperum** Calvert. A few specimens were taken during July. This is quite similar to *signatum*, but seems to occur more frequently in the grassy part of the swamp. One male was taken on a shrubby hillside on the south side of the lake.

37. **Enallagma exsulans** Hagen. Quite common throughout the summer, occurring in the cattails and bulrushes at the edge of the water, and occasionally in the fields and woods near the lake.
38. **Enallagma antennatum** Say. This species was quite common along Buckongahelas and Bluejacket Creeks, where it was found flying over the vegetation at the water's edge.
39. **Enallagma carunculatum** Morse. Quite abundant throughout the summer. It occurs in the cattails and bulrushes at the edge of the lake, back farther in the marshes, and occasionally in the woods and fields near the lake. Oviposition occurs in submerged vegetation near the water's edge.
40. **Enallagma doubledayi** Selys. Two males, June 26, taken on a grassy and shrubby hillside near the lake.
41. **Enallagma aspersum** Hagen. One male, July 3, in a swampy woods.
42. **Enallagma traviatum** Selys. Fairly common up until about July 3, occurring in situations similar to those in which *exsulans* and *carunculatum* are found.
43. **Ischnura posita** Hagen. Found occasionally throughout the summer in the grassy parts of the swamps around the lake, and in the swampy vegetation along streams.
44. **Ischnura verticalis** Say. Very abundant throughout the summer, occurring everywhere any other species was found. This was the most abundant damselfly observed during the summer.
45. **Anomalagrion hastatum** Say. One male, August 9, taken in a swampy woods.

Of these 45 species, four are new records for the state: *Aeschna umbrosa* (No. 2), *Nannothemis bella* (No. 4), *Argia bipunctulata* (No. 28), and *Enallagma vesperum* (No. 36). I am sure that *A. umbrosa* and *E. vesperum* have been taken in the state before, though I can find no published records to that effect. The record of *N. bella*, however, is certainly new, and that of *A. bipunctulata* appears to be the first record of its capture west of the Appalachian Mountains.

BOOK REVIEWS.

A DICTIONARY OF GREEK AND LATIN COMBINING FORMS USED IN ZOOLOGICAL NAMES. By EDMUND C. JAEGER. Charles C. Thomas, Publisher, Springfield, Ill.

Students in Biology will welcome this assemblage of technical terms showing the derivation and combining forms which are applicable in many different branches of Biology.

This book of one hundred pages includes the root form for more than one thousand words of common technical use.

KINETIC SPACE AND ITS SPECULATIVE CONSEQUENCES. By DR. R. W. MANLEY. Published by the author at Cleveland, Ohio.

Includes a discussion of the problems of space and contains a tribute to the work of Johann Kepler.

REACTIONS AND SYMBOLS OF CARBON COMPOUNDS. By T. CLINTON TAYLOR. Published by the Century Co., New York.

This work is a detailed presentation of the reactions and symbols used in organic chemistry, the aim of the book being to simplify the study of symbols by emphasizing the reaction and explaining fully the steps taken to formulate the symbol.

BLATCHLEYANA: A LIST OF THE PUBLISHED WRITINGS OF W. S. BLATCHLEY, A. B., A. M., LL. D., Together with a Chronology of His Life; The Fixation of Types of New Genera and Species Described by Him.

Doctor Blatchley has here brought together a complete list of titles of his papers and record of the new genera and species described by him with statement of their present location. It also includes a number of quotations from his various published books.

THE GALL WASP GENUS CYNIPS, A STUDY IN THE ORIGIN OF SPECIES. By ALFRED C. KINSEY. Waterman Institute for Scientific Research, Publication No. 42; Contribution from the Department of Zoology, Indiana University, No. 220 (Entomological Series No. 7).

This volume of 577 pages, including over four hundred figures, is much more than a monograph of the genus as it treats in a very exhaustive manner of problems of distribution, affinities and especially the lines of evolution for the different species with special reference to the American fauna. It is the outcome of twelve years of travel, research, and taxonomic studies and may well serve as a model for other taxonomic studies.

H. O.

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